

Relationship between the Quantum Efficiencies of Photosystems I and II in Pea Leaves¹

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ABSTRACT

The irradiance dependence of the efficiencies of photosystems I and II were measured for two pea (*Pisum sativum* [L.]) varieties grown under cold conditions and one pea variety grown under warm conditions. The efficiencies of both photosystems declined with increasing irradiance for all plants, and the quantum efficiency of photosystem I electron transport was closely correlated with the quantum efficiency of photosystem II electron transport. In contrast to the consistent pattern shown by efficiency of the photosystems, the redox state of photosystem II (as estimated from the photochemical quenching coefficient of chlorophyll fluorescence) exhibited relationships with both irradiance and the reduction of P-700 that varied with growth environment and genotype. This variability is considered in the context of the modulation of photosystem II quantum efficiency by both photochemical and nonphotochemical quenching of excitation energy.

The well established organization of the electron transport system of higher plant thylakoids implies a close coordination of the activities of PSI and PSII in linear electron flow (13, 28). Although considerable efforts have been applied for the characterization of the detailed structure and functions of PSI and PSII, remarkably little attention has been given to the potential regulatory mechanisms needed to coordinate PSI and PSII activities. In this paper we examine the relationships between PSI and PSII photochemical activities in leaves using noninvasive spectroscopic techniques.

Under conditions of increasing irradiance, the quantum efficiencies of both PSI and PSII decline. Oxidized P-700² (P-

700⁺) is as good a quencher of excitation energy present in PSI as is reduced P-700 (P-700⁰) (25), but whereas quenching by P-700⁰ results in electron transport from PSI, quenching by P-700⁺ results only in thermal deactivation of the excitation energy. Consequently, the quantum efficiency of PSI is given by the degree of reduction of the P-700 pool (*i.e.* the amount of P-700⁰ relative to the total amount of P-700). Measurements of the redox state of P-700 *in vivo* have shown that the quantum efficiency of PSI is linearly related to the quantum efficiency for CO₂ fixation when photorespiration is suppressed (28). With increasing irradiance the P-700 pool becomes progressively oxidized (15, 16, 28), and hence the quantum efficiency of PSI falls. The situation for PSII is complicated by the multiplicity of ways that PSII quantum efficiency can be modified (5, 16). The resolution of Chl fluorescence *in vivo* (which is largely from PSII) in terms of photochemical (q_Q) and nonphotochemical quenching (q_{NP}) has been described by Bradbury and Baker (3) and Deitz *et al.* (8). With increasing irradiance, q_Q declines and q_{NP} increases (8) but not in a way that can be simply related to the decline of Φ_{PSII} (the quantum efficiency for electron transport by PSII) (29). Recently, Genty *et al.* (11) have shown that it is possible to estimate Φ_{PSII} from measurements of Chl fluorescence as it is the product of q_Q and Φ_{exc} (the excitation capture efficiency of PSII). The term q_Q is a measure of the proportion of PSII reaction centers that are capable of photochemistry and is approximately equal to the redox state of PSII reaction centers (18, 21). The Φ_{exc} is an estimate of how efficiently excitation energy trapped by PSII is transferred to the PSII reaction centers and how efficiently open PSII centers reduce Q; Φ_{exc} can be estimated from the ratio of variable to maximal PSII fluorescence (F_v/F_m) (2, 6, 19).

The sequential arrangement of photosystems II and I in noncyclic electron transport (27) suggests that at steady state changes in the efficiency of either photosystem should be reflected by a change in the efficiency of the other photosystem. So far, only measurements of a qualitative nature have been made and these suggest that the efficiencies of both photosystems are similar *in vivo* (1). Any simple relationship between the quantum efficiency of PSI and PSII could be complicated due to cyclic flow around PSI, cyclic flow around PSII (10, 17), an imbalance in the rate of excitation (9, 22), and population size (24) of the reaction centers of both photosystems, inactive PSII centers, (12), and fluxes of electrons from the reducing side of PSII to O₂ (4, 23). Parallel

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² Abbreviations: P-700, general term for all P-700; P-700⁰, reduced P-700 (this is P-700 in the zero oxidation state and is termed 'reduced' because of its relationship with P-700⁺); P-700⁺, oxidized P-700; q_Q , photochemical quenching of Chl fluorescence; Φ_{exc} , efficiency of excitation capture by open PSII centers; Φ_{PSI} and Φ_{PSII} , quantum efficiencies for electron transport by photosystems I and II, respectively; F_0 , level of Chl fluorescence with all PSII traps open; F_s , steady state level of Chl fluorescence; F_m , level of Chl fluorescence when all PSII traps are closed; Q_A , primary electron accepting plastoquinone of PSII; PAQF, photosynthetically active quantum flux.

measurements of the decline of Φ_{PSII} and Φ_{PSI} (the quantum efficiency of PSI) with increasing irradiance will allow the relationship between the two photosystems to be expressed quantitatively.

The quantum efficiency of PSII can be monitored conveniently *in vivo* using fluorescence parameters. Also the quantum efficiency of PSI can be monitored *in vivo* by using light-induced absorbance changes at 820 nm (15). By combining fluorescence and 820 nm absorbance measurements in a single apparatus, both Φ_{PSII} (via measurements of q_Q and Φ_{exc}) and Φ_{PSI} can be measured simultaneously in leaf tissue.

A decline of q_Q with increasing irradiance has been amply demonstrated in leaves of many taxa (8, 28). However, we show that when peas are grown under cold conditions the q_Q of some varieties remains almost constant with increasing irradiance. We also demonstrate that Φ_{PSII} and Φ_{PSI} decline in parallel as irradiance is increased and that the decline of Φ_{PSII} efficiency is attributable to a decrease of q_Q and a rise of q_{NP} . Our data indicate that a parallel decline of Φ_{PSII} and Φ_{PSI} with increasing irradiance is a consistent feature among different genotypes of pea grown in contrasting environments. However, the irradiance response of q_Q and its relationship with Φ_{PSI} is a variable feature of such plants. Data are presented here from three varieties of pea, two of which were grown under cold conditions. One of the varieties retains a strong negative correlation between q_Q and irradiance when grown under cold conditions, whereas for another variety q_Q is independent of irradiance when grown under cold conditions. For both of these varieties the efficiencies of both PSII and PSI decline markedly with increasing irradiance. The significance of these data in relation to the control of photosynthetic electron transport is discussed.

MATERIALS AND METHODS

All the measurements were made on peas (*Pisum sativum* [L.]) grown in a growth cabinet under warm conditions (25°C day, 15°C night, 16 h photoperiod 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ irradiance) or cold conditions (5°C day, 5°C night, 16 h photoperiod, 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ irradiance). Varieties JI 799, JI 1345 (John Innes Institute *Pisum* germplasm collection), and BC1/8RR were used. All plants were grown in 70% John Innes No. 1 potting compost/30% chicken grit in 12.5 cm pots. The youngest fully expanded leaves were chosen for measurement.

Chlorophyll fluorescence was measured using a modulated technique (19, 26). Modulated chlorophyll fluorescence was produced by irradiating the leaf with a weak ($\sim 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF modulated ($\sim 500 \text{ Hz}$) red excitation beam (peak wavelength 660 nm). A PIN photodiode (S1223, Hamamatsu Photonics, Hamamatsu City, Japan) screened by RG9N (Schott, Mainz Fed. Rep. Germany) and Wratten 87 filters was located under the leaf and was used to detect the Chl fluorescence. This detector was also used to detect the modulated 820 nm measuring beam used for measurements of P-700 oxidation (15). The composite signal from the photodiode containing the modulated Chl fluorescence and ΔA_{820} data was processed in laboratory built demodulators after the design of Harbinson and Woodward (15), and the fluorescence and ΔA_{820} signals were recorded on a chart recorder. The actinic light used was obtained from an array of light

emitting diodes (H-2K, Stanley, Tokyo, Japan: λ_{max} 660 nm) and identical results were obtained using broadband light. The leaf was exposed to the lowest irradiance first and then to progressively higher irradiances; exposure to each to irradiance lasted about 20 min, which was long enough to allow a new steady state to be reached. Throughout the measurements, the leaf was held at 22 to 23°C and exposed to a gaseous phase of 350 ppm CO_2 and 20% O_2 in N_2 .

During irradiation, absorbance changes occur around 820 nm for reasons other than P-700 oxidation. Following a light-dark transition, P-700⁺ is reduced with a half-time of 5 ms (14), whereas the decay of the absorbance change due to other processes is much slower ($t_{1/2}$ in the order of seconds). To separate absorbance changes due to P-700 oxidation/reduction from those caused by other processes, the actinic light was removed for 10 s every 100 s and the fast absorbance decrease occurring in the dark was taken to represent that due to P-700⁺ reduction. To obtain an estimate of the fluorescence level corresponding to complete reduction of Q_A (F_m), the leaf was subjected to a brief (1–2 s) saturating pulse of broadband white light with an irradiance of 7500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF. The leaf was irradiated with 700 nm radiation ($\sim 35 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 5 s) during the dark interval prior to determination of F_m to completely oxidize any Q_A and obtain an accurate estimate of F_o . The steady state fluorescence level (F_s) was taken as the level of fluorescence immediately before the saturating pulse of light was applied. The ΔA_{820} corresponding to complete oxidation of RC_1 was estimated by subjecting the leaf to a combination of 660 nm (750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF) and 700 nm radiation. After 60 s, the 660 nm radiation was removed, and following a further 90 s of irradiation with only 770 nm radiation this was also removed and the ensuing absorbance change measured. This process was repeated for a range of irradiances at 700 nm and the reciprocal of the irradiance at 700 nm was plotted against absorbance change. The relationship obtained by linear regression was then extrapolated to give the absorbance change corresponding to an infinite irradiance at 700 nm. This was taken to be the absorbance corresponding to complete oxidation of P-700 ($\Delta A_{820} [\text{max}]$). Whenever possible, the absorbance change obtained from the 660 nm irradiance experiments was treated similarly, and the absorbance changes at infinite irradiance obtained by extrapolation (as above) were found to be in close agreement ($\pm 5\%$) with the result obtained using 700 nm radiation.

The percent oxidation of P-700 was determined from $100 \times (\Delta A_{820} / \Delta A_{820} [\text{max}])$. The efficiency of excitation capture by PSII was determined from $(F_m - F_o) / F_m$, the overall quantum efficiency of PSII was calculated from $(F_m - F_s) / F_m$ (9), and q_Q was determined from $(F_m - F_s) / (F_m - F_o)$ (6).

RESULTS

Three sets of data are presented: one example is from a warm-grown plant of line BC1/8RR (Fig. 1), one is from a cold-grown plant of variety JI 799 (Fig. 2), and the third is from a cold-grown plant of variety JI 1345 (Fig. 3). The results are for a single leaf in each case; however, similar data were obtained from replicate leaf samples.

The results from warm-grown pea plant BC1/8RR are

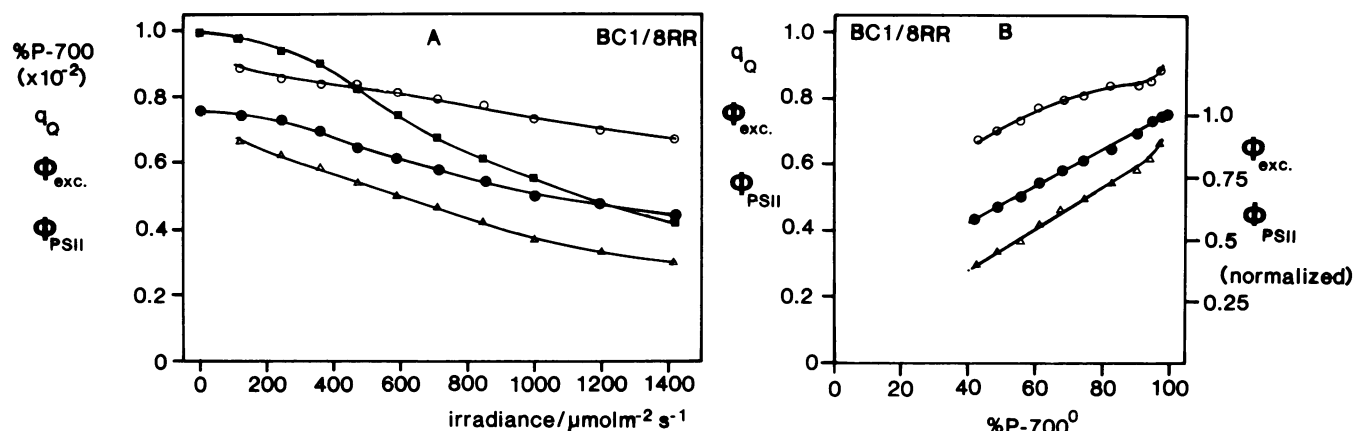


Figure 1. A, The irradiance dependence of percentage reduction of P-700 (\blacksquare), q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea line BC1/8RR; B, the relationship between the percentage oxidation of P-700 and q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea line BC1/8RR. The right hand ordinate shows the normalized scale for Φ_{exc} and Φ_{PSII} .

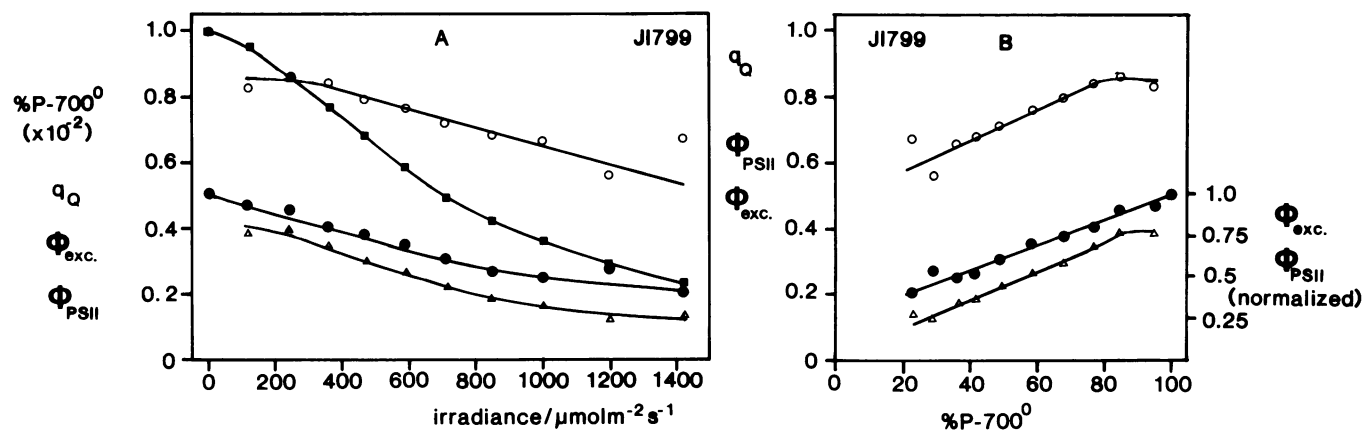


Figure 2. A, The irradiance dependence of percentage reduction of P-700 (\blacksquare), q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea variety JI 799; B, the relationship between the percentage oxidation of P-700 and q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea variety JI 799. The right hand ordinate shows the normalized scale for Φ_{exc} and Φ_{PSII} .

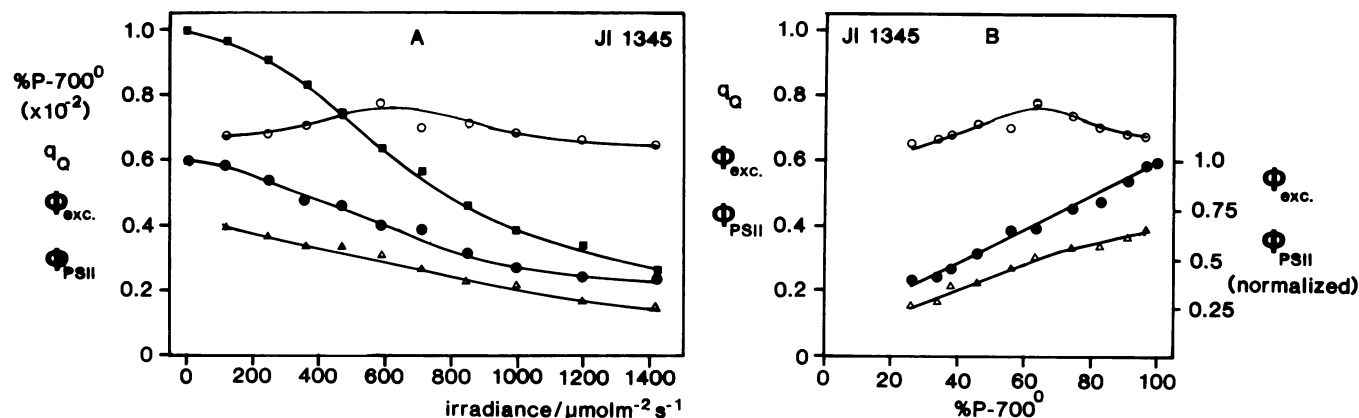


Figure 3. A, The irradiance dependence of percentage reduction of P-700 (\blacksquare), q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea variety JI 1345; B, the relationship between the percentage oxidation of P-700 and q_Q (\circ), the excitation capture efficiency of PSII, Φ_{exc} (\bullet), and the overall efficiency of PSII, Φ_{PSII} (\triangle) for pea variety JI 1345. The right hand ordinate shows the normalized scale for Φ_{exc} and Φ_{PSII} .

typical of other data obtained from warm-grown control plants of other varieties (data not shown). The pool of P-700⁰ and q_Q decrease with increasing irradiance (Fig. 1A). The efficiency of excitation capture by PSII (Fig. 1A) declines with increasing irradiance in parallel with the decrease in P-700⁰. The overall Φ_{PSII} (Fig. 1A) also declines, but more sharply than the Φ_{exc} as would be expected given that it is the product of Φ_{exc} and q_Q . The relationship between q_Q and P-700⁰ (Fig. 1B) appears to be comprised of two phases; q_Q initially declines rapidly with decreasing P-700⁰ and this phase is followed by a gentler curvilinear relationship between q_Q and P-700⁰. The Φ_{exc} is very closely correlated with the oxidation of P-700 (Fig. 1B) and the calculated maximum efficiency of excitation capture (0.768), determined by extrapolation of the data line to the origin, is very close to the efficiency of excitation capture by the dark-adapted leaf (0.759). The decline of Φ_{PSII} is linearly related to the accumulation of P-700⁺ (Fig. 1B) except at low values of P-700⁺, where a more rapid loss of PSII efficiency can be inferred from the data.

The data for cold-grown pea variety JI 799 (Fig. 2, A and B) are qualitatively similar to those of warm-grown line BC1/8RR (Fig. 1, A and B). When grown in the cold, leaves of variety JI 799 continue to show a marked decrease in q_Q with increasing irradiance, and they also show a marked loss of Chl when grown at high levels of irradiance at low temperatures (data not shown). The data obtained from a leaf of this variety are included since they are representative of a specific type of response associated with leaf growth at low temperatures. The variability in the fluorescence data from such leaves is largely due to a high degree of nonphotochemical quenching of fluorescence and the reduced level of Chl. The pool of P-700⁰ decreases more rapidly with irradiance and is much less sigmoidal than for warm grown pea variety BC1/8RR. The q_Q value also shows a greater decrease with irradiance relative to the BC1/8RR variety though this increase is less marked than for P-700⁰. The Φ_{exc} declines more sharply than for var BC1/8RR (Fig. 2A). The overall Φ_{PSII} in the cold grown JI 799 is less, at any irradiance than for var BC1/8RR due to the lower Φ_{exc} and lower q_Q . Relative to decreasing P-700⁰, q_Q decreases linearly (Fig. 2B), although a phase in which q_Q decreases rapidly with only a slight loss of P-700 can be inferred from the data at very low levels of irradiance (Fig. 2B). The Φ_{exc} is again very closely correlated to the accumulation of P-700⁺ (Fig. 2B). The calculated Φ_{exc} when all P-700 is reduced is 0.493, which is considerably less than for var BC1/8RR. As is the case for var BC1/8RR, the decline of Φ_{PSII} (Fig. 2B) is linearly related to the loss of P-700⁰ except at high values of P-700⁰.

The data obtained from a leaf of a cold-grown plant of var JI 1345 and shown in Figure 3 are typical of plants of varieties in which q_Q is independent of largely independent of irradiance when they are cold grown. A sharp decline in the value of q_Q from 1.0 (the dark adapted state) to 0.67 at 120 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF can be inferred from the data; following this decline, a small increase in q_Q up to about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF is observed (Fig. 3A). At irradiances above 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAQF q_Q decreases slightly. A decline of Φ_{exc} is again closely correlated with the decline of P-700⁰ accumulation (Fig. 3, A and B). The Φ_{PSII} when all P-700 is reduced is

calculated to be 0.58, which is again intermediate between the varieties BC1/8RR and JI799. The relationship between Φ_{PSII} and of Φ_{PSI} (% P-700⁰) (Fig. 3B) is complex as would be anticipated from the monophasic relationship between Φ_{exc} and the P-700⁰ and complex relationship between q_Q and P-700⁰.

DISCUSSION

The data presented in this paper show that the response of q_Q to increasing irradiance is quite variable and depends on the genotype and growth conditions of the leaf. It is even possible for q_Q to increase with irradiance at the same time as the quantum efficiency of thylakoid noncyclic electron transport was decreasing (Fig. 3B). In relation to the redox state of P-700, q_Q can adopt a range of relationships ranging from a positive correlation (Fig. 2B) to a negative correlation (Fig. 3B). Nonetheless, Φ_{PSII} is very well related to the degree of oxidation of P-700 over most of the range of data. This is as would be expected. Photosystems II and I operate sequentially in noncyclic transport, and at steady state the fluxes of electrons entering and leaving any portion of the thylakoid electron transport chain must balance; any imbalance will result in compensatory increases or decreases in the quantum efficiencies of one or other systems to restore this balance of flux. In the data shown, Φ_{PSII} appears to decline to zero when approximately all P-700 is oxidized and Φ_{PSI} is zero.

The model of PSII function proposed by Genty *et al.* (11) distinguishes between Φ_{exc} , which is a measure of the supply of energy reaching the PSII reaction centers, and q_Q of these centers, which is also a measure of the redox state of PSII. The data clearly show that large declines in Φ_{exc} can occur with increasing irradiance (Figs. 2A and 3A). The nonphotochemical quenching represented by this decrease in Φ_{exc} in combination with q_Q determines the overall efficiency of PSII (Φ_{PSII}). Neglecting fluxes to O₂ (which are small [23]), the flux of reducing equivalents from PSII must equal the flux of reducing equivalents from PSI to NADP⁺. As Φ_{PSI} declines with increasing irradiance, then so must Φ_{PSII} . The drop in the efficiency of PSII will be shared between a fall in Φ_{exc} and a fall in q_Q , which is also the proportion of PSII reaction centers that are nonreduced and open.

These data clearly show that q_Q has no consistent correlation with P-700 oxidation (or quantum efficiency of noncyclic electron transport). However, the decline of Φ_{PSII} , which is the product q_Q and Φ_{exc} , is very well related to the decline of Φ_{PSI} . The decline of Φ_{exc} is a manifestation of nonphotochemical quenching of PSII excitation. These data support the suggestion (29) that regulation of PSII efficiency by nonphotochemical quenching of excitation energy can operate to a substantial degree to reduce the excitation energy reaching the reaction centers of PSII.

The correlation between the oxidation of PSI reaction centers and the decline of the Φ_{exc} (and therefore the rise of nonphotochemical quenching) suggests that in the cases represented here the accumulation of P-700⁺ is closely coordinated with the degree of nonphotochemical quenching in PSII.

The coordination between the fall of Φ_{PSI} , the fall of Φ_{exc} , and the need for the efficiencies of PSII and PSI to be balanced

allow the different irradiance responses of q_Q to be understood. Much of the regulation of PSII occurs via nonphotochemical quenching; any further imbalance between PSII and PSI is absorbed by a change in the photochemical efficiency of PSII and is manifested by a change in q_Q . Depending on the precise relationship between nonphotochemical quenching and the oxidation state of the P-700 pool, q_Q can adopt a range of relationships with irradiance on P-700 oxidation to produce a balance between the two photosystems. The striking and apparently ubiquitous relationship between Φ_{PSI} and Φ_{exc} clearly warrants further serious investigation.

The relatively rapid fall in q_Q and Φ_{PSII} that occurs at low irradiances with only a small drop in Φ_{PSI} may be due to the presence of inactive PSII centers (12) or to over excitation of PSII relative to PSI at the excitation wavelength used (9, 18).

The variability of the relationship between the redox state of PSII and irradiance, and, by implication, the relationship between PSII and PSI redox states can be understood as a consequence of the interaction of (a) the resolution of PSII efficiency in terms of excitation capture efficiency and q_Q , (b) the coordination of the excitation capture efficiency of PSII and the oxidation state of P-700, and (c) the requirement to balance the electron fluxes within the thylakoid electron transport chain. In leaves of var. JI 1345, the lack of a simple linear relationship between Φ_{PSI} and Φ_{PSII} , as is found in vars BC1/8RR and JI 799 may suggest that other processes may affect the coupling of PSII and PSI.

The contrasting behavior of q_Q discussed in this paper highlights the importance of considering both photochemical and nonphotochemical quenching of excitation energy when attempting to evaluate changes in the quantum efficiency of PSII. Taken in isolation, q_Q cannot be used to estimate Φ_{PSII} . The relative stability of q_Q over a range of irradiances observed among many cold-grown pea plants may have a role in protecting the leaf from oxidative stress and damage and this is currently under investigation (4, 20, 23).

The data from the two cold-grown varieties show a greater accumulation of P-700⁺ with increasing irradiance (Figs. 2A and 3C) than do those from the warm-grown variety (Fig. 1A). Prolonged cold exposure also causes a marked reduction in maximum rate of CO₂ fixation (data not shown). This is consistent with the observation of Weis *et al.* (28) that the quantum efficiency of CO₂ fixation in 2% O₂ is a function of the degree of oxidation of PSI. Both cold-grown varieties show a reduced excitation capture efficiency for PSII at zero irradiance relative to the warm-grown variety. The excitation capture efficiency at zero irradiance equates to F_v/F_m , and this ratio has been shown to be related to the quantum efficiency for O₂ evolution *in vivo* (7). A decline of the apparent quantum efficiency for CO₂ fixation does occur following the prolonged cold growth of peas (data not shown), and this is consistent with decline in quantum efficiency implied by the PSII excitation capture efficiency.

This study has clearly shown:

(a) The importance of nonphotochemical quenching in controlling the quantum efficiency: frequently this has a greater effect on PSII quantum efficiency than does the loss of photochemical quenching following Q_A⁻ accumulation.

(b) The need to consider both photochemical and nonphotochemical quenching as determinants of quantum efficiency of PSII.

(c) The quantum efficiencies of PSII and PSI are consistently correlated as would be expected from their electrochemical relationship in the noncyclic electron transport chain.

(d) The magnitude of nonphotochemical quenching is closely correlated with the accumulation of P-700⁺: this results in a coordination of the decline of the quantum efficiency of PSI with the decrease of the efficiency of excitation capture by PSII.

(e) The redox state of PSII does not display any consistent relationship with the oxidation of P-700.

These findings imply that a rigid coordination of PSI and PSII activities exists in the thylakoid membranes *in vivo*. Also, it is evident that a strict correlation exists between the processing of absorbed light energy by PSII complexes and the oxidation state of PSI reaction centers. This remarkable correlation may be indicative of the existence of a previously unidentified regulatory mechanism for coordinating PSI and PSII activities in thylakoids *in vivo*.

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